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Cranial morphology and taxonomy of South African Tapinocephalidae (Therapsida: Dinocephalia): the case of *Avenantia* and *Riebeeckosaurus*

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Tapinocephalid dinocephalians comprise a large component of Middle Permian herbivorous tetrapod biodiversity and are significantly abundant in the Karoo rocks of South Africa. In order to understand the effect of the alleged Middle Permian extinction in the terrestrial record of amniotes a clear understanding of the taxonomic diversity of this group is essential. The tapinocephalids *Avenantia kruisvleiensis* and *Riebeeckosaurus longirostris* have in the past been distinguished by a set of characters, including differences in the snout length which was previously interpreted as a key diagnostic character. Further preparation of the material attributed to these species shows that the purported distinguishing characters, such as snout length, low intertemporal crest, and surface thickening of the parietal represent postmortem deformation (including distortion and weathering) or can be interpreted as individual or ontogenetic variation. Accordingly *A. kruisvleiensis* is synonimized with *R. longirostris*.

Keywords: herbivorous Dinocephalia, Tapinocephalidae, *Tapinocephalus* Assemblage Zone, Karoo Basin, South Africa.

INTRODUCTION

Dinocephalians formed the major component of the Middle Permian terrestrial tetrapod diversity as is evidenced by the large number of taxa of herbivorous tapinocephalids from the rocks of the Abrahamskraal Formation, Karoo Supergroup of South Africa (Rubidge *et al.* 1995; Smith *et al*. 2012). Several of these taxa are based on fragmentary holotypes in which diagnostic characters are hardly evident, suggesting that the number of tapinocephalid genera from the Karoo may be inflated. In the most recent taxonomic revisions of dinocephalians, Boonstra (1969) recognized four and King (1988) two groups of tapinocephalids, in which the snout length was considered one of the main diagnostic characters.

Avenantia and *Riebeeckosaurus* are monospecific tapinocephalid genera from the Lower Beaufort Group of the Karoo Basin. Boonstra (1952a) described *Riebeeckosaurus longirostris*, represented by the holotype (a distorted and fragmented cranium with lower jaw) and a referred specimen (the dorsal portion of cranium), as a long-snouted species. Boonstra (1952b) described *Avenantia kruisvleiensis* as a *Moschops* like tapinocephalian with a short-snout. Both species are described has having large and roomy opening [there is inconsistency regarding this character because in the same contribution, Boonstra (1952: 254) referred to the temporal opening of *A. kruisvleiensis* as small]. Despite the fact that the materials of both genera lack a snout, Boonstra (1952a) interpreted the holotype of *R. longirostris* as being long-snouted, based on the length of the lower jaw. The author considered the species as morphologically intermediate between the short-snouted Moschopidae and long-snouted Mormosauridae as described in Boonstra (1936) but did not allocate *R. longirostris* in any particular subgroup. Later, *A. kruisvleiensis* was considered a member of the Moschopidae by both Haughton & Brink (1954) and Boonstra (1957), and *R. longirostris* a member of the also short-snouted family Tapinocephalidae by the former authors. In 1963 Boonstra founded the subfamily Riebeeckosaurinae for *R. longirostris* while Orlov (1964) assigned *R. longirostris* to the family Mormosauridae, which was defined as having forms with a relatively longer snout and lesser pachyostosis than the members of the Tapinocephalidae. Barghusen (1975) interpreted the dentary of the holotype of *R. longirostris* as having been displaced forward in relation to the post-dentary bones, casting doubt on Boonstra's interpretation of a long snout for the taxon, and suggested the replacement of *R. longirostris* into the subfamily Moschopinae of Boonstra (1969). Van den Heever & Grine (1981) and King (1988) kept *Riebeeckosaurus longirostris* in the tribe Riebeeckosaurini, whereas *Avenantia kruisvleiensis* was included by King (1988) in the tribe Tapinocephalini (a combination of the previous subfamilies Moschopinae and Tapinocephalinae, e.g. Boonstra 1969).

In this paper we present a re-evaluation of the taxonomic disparity between *A. kruisvleiensis* and *R. longirostris* as the materials comprising these two genera has not been studied in detail since Boonstra's (1952a,b) original descriptions. Additional preparation of the specimens has revealed important new information and enabled a detailed redescription of the material attributed to these species. This re-evaluation is part of a broader project to review the alpha taxonomy of the Tapinocephalidae as a tool contributing to the assessment of terrestrial vertebrate diversity in the Middle Permian.

MATERIAL AND METHODS

The holotype specimens, SAM-PK-003400 (*Riebeeckosaurus longirostris*, Figs 1–2), SAM-PK-009166 (*Avenantia*

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kruisvleiensis, Figs 3–4) and referred specimen SAM-PK-011955 (*R. longirostris,* Fig. 1) were mechanically prepared with the aid of airscribes. Comparative materials utilized include specimens of the short-snouted tapinocephalids *Moschops, Criocephalosaurus* and *Tapinocaninus*: SAM-PK-11582 (holotype of *M. koupensis*), SAM-PK-K0319 (identified here as *Moschops* but it is registered as *Criocephalosaurus* in the SAM database), NMQR 2987 (*Tapinocaninus pamelae* holotype), NMQR 2985 and NMQR 2986 (*T. pamelae* referred). Descriptive terminology for the margins of the teeth follows Heckert (2004).

REVISED DESCRIPTIONS

Riebeeckosaurus longirostris

In the holotype (SAM-PK-003400) both the cranium and the lower jaw were previously reconstructed from several weathered, poorly fitting fragments. It is evident that the skull has suffered postmortem distortion, which affected the width of the skull roof and caused the occiput to be pushed relatively forward. The left side of the skull is less distorted than the right. Re-examination indicates that the width between the squamosals is greater than reconstructed by Boonstra (1952a). The skull of the referred specimen (SAM-PK-011955), which comprises the posterior portion of the skull roof (Fig. 1A), is larger than that of the holotype. Both specimens display a moderate degree of pachyostosis of the skull roof, a feature which is clearly demonstrated by the thick, robust nature of the postorbital bar (width of 100 mm in the holotype). The temporal opening in the holotype is large and roomy, with the anteroposterior diameter being larger than the dorsoventral diameter. The palate is not preserved in either of the specimens.

Skull roof and lateral view

In both specimens of *Riebeeckosaurus* the inter-temporal area is a narrow crest produced by thin posterior projections of the parietal (Fig. 1A,B). These form the dorsomedial border of the temporal opening and curve backwards, but not at a sharp angle as described by Boonstra (1952a). The squamosal forms the posterior and lateral borders of the relatively large temporal opening. The contribution of this bone to the posterior border of the temporal opening is not fully preserved in the available specimens (in contrast to Boonstra 1952a, fig. 2, illustration of the squamosal on the posterior branch of the temporal opening in the holotype). This bone, as evidenced by the medial portion of the right temporal opening of SAM-PK-011955, makes up a short section of the posterior dorsomedial border. Posteroventrally, the squamosal extends to the base of the skull. Because of the weathered nature of the zygomatic arch, the contact of the squamosal with the jugal is not evident on the left side and only the posterior portion of the zygoma is preserved on the right (Fig. 1C,D).

The parietal forms a narrow exposure in the form of a crest in the intertemporal region, broadens to its greatest width in line with the pineal foramen, and tapers anteriorly to a point on the midline between the frontals. In both specimens the pineal opening is situated on a slightly raised boss in the centre of the parietals (Fig. 1A,B).

The frontal forms the greatest portion of the skull roof in the interorbital region, contributing to the orbital border in both specimens (Fig. 1A,B,D), and extending posteriorly between the parietal and postfrontal to make a small contribution to the temporal opening (Fig. 1A,B). An elongated midline depression on the skull roof extends along the frontals but is absent from the nasals anteriorly, and the parietals posteriorly. The partially preserved prefrontal is a large bone which contributes to the anterodorsal margin of the orbit, and contacts the frontal posteriorly, and the narrow posterior projection of the nasal medially. In SAM-PK-011955, the posterior ends of the two thin elongated nasals have a short posterior contact with the frontal (Fig. 1A). An anteroposteriorly elongated postfrontal contributes to the anterior border of the temporal opening and the posterodorsal margin of the orbit (Fig. 1A,B), and is in contact with the frontal medially and the postorbital on the lateral side. The postorbital meets the squamosal at the base of the postorbital bar as it is evident in the holotype (Fig. 1D).

The cranio-mandibular joint, as preserved, is located below the mid-point of the orbit. This rather anterior placement of the jaw joint seems to be the result of dorsoventral deformation of the skull.

Occipital view

The occiput in the holotype is mostly complete, but poorly preserved and reconstructed from weathered fragments (Fig. 1E) and, as a result, sutural pathways are not clear. There is a striking transverse thickening which extends across the occiput at a level corresponding to the lower limit of the tabular, parallel to the dorsal border of the supraoccipital (Fig. 1E). Dorsally the parietals have a small exposure on the occiput above the postparietal. The postparietal is a prominent, long rectangular unpaired bone on the occiput, which has a long sinuous contact with the parietal dorsally and the supraoccipital ventrally, and a short contact with the tabular laterally. The latter is a large ovoid paired element with a well-developed ventral projection forming the dorsolateral border of the occiput. Dorsomedially the tabular has a short contact with the parietal, ventromedially with the postparietal, and laterally with the squamosal. There is a long sutural contact with the supraoccipital in which a thin ventrolateral tongue of the tabular extends between the supraoccipital and squamosal. The squamosal is a massive bone, which forms a large part of the lateral side of the occiput, and has a prominent dorsoventrally orientated squamosal sulcus. It contacts the tabular dorsomedially, the paraoccipital process of the opisthotic medially, and the dorsal process of the quadrate anteriorly.

Lower jaw

The lower jaw has the complete left ramus, which is composed of five fragments, and the anterior symphysial portion of the right ramus (Fig. 2C,D). The fact that the right symphysial region is much shorter, but higher, than the left indicates significant deformation of the material

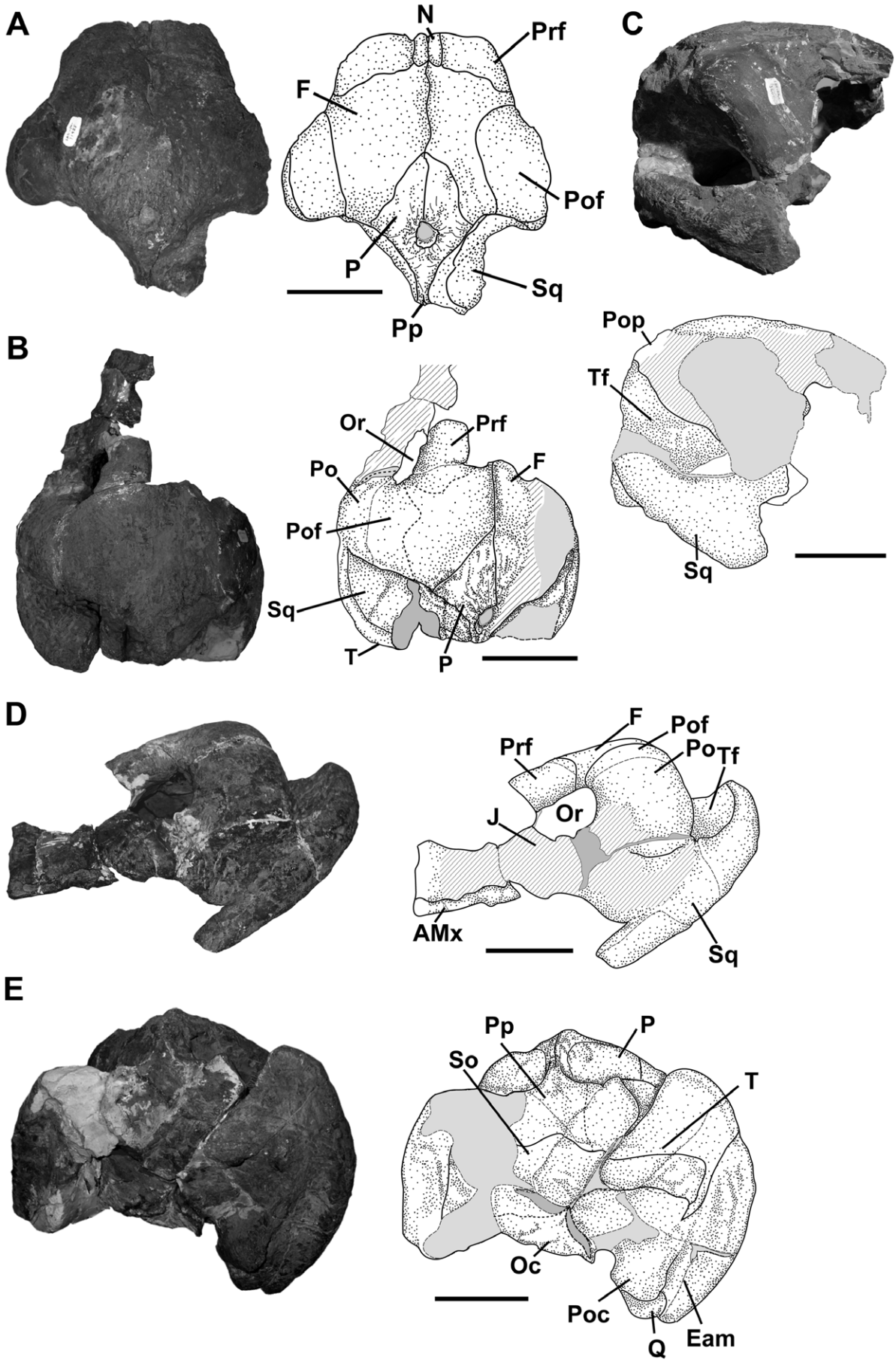

Figure 1. Photographs and drawings of dorsal view (**A**) of SAM-PK-011955 (*Riebeeckosaurus longirostris* referred specimen) and dorsal (**B**), right (**C**), left (**D**), and occipital (**E**) views of SAM-PK-003400 (holotype of *R. longirostris*). Solid lines are visible and dashed lines are interpreted sutures; narrow dashed lines are borders of bone fragments; dark grey areas shows damaged bone surfaces, light grey are reconstructed areas and matrix infilling; diagonal lines represent weathered bone surfaces. Scale bars = 10 cm.

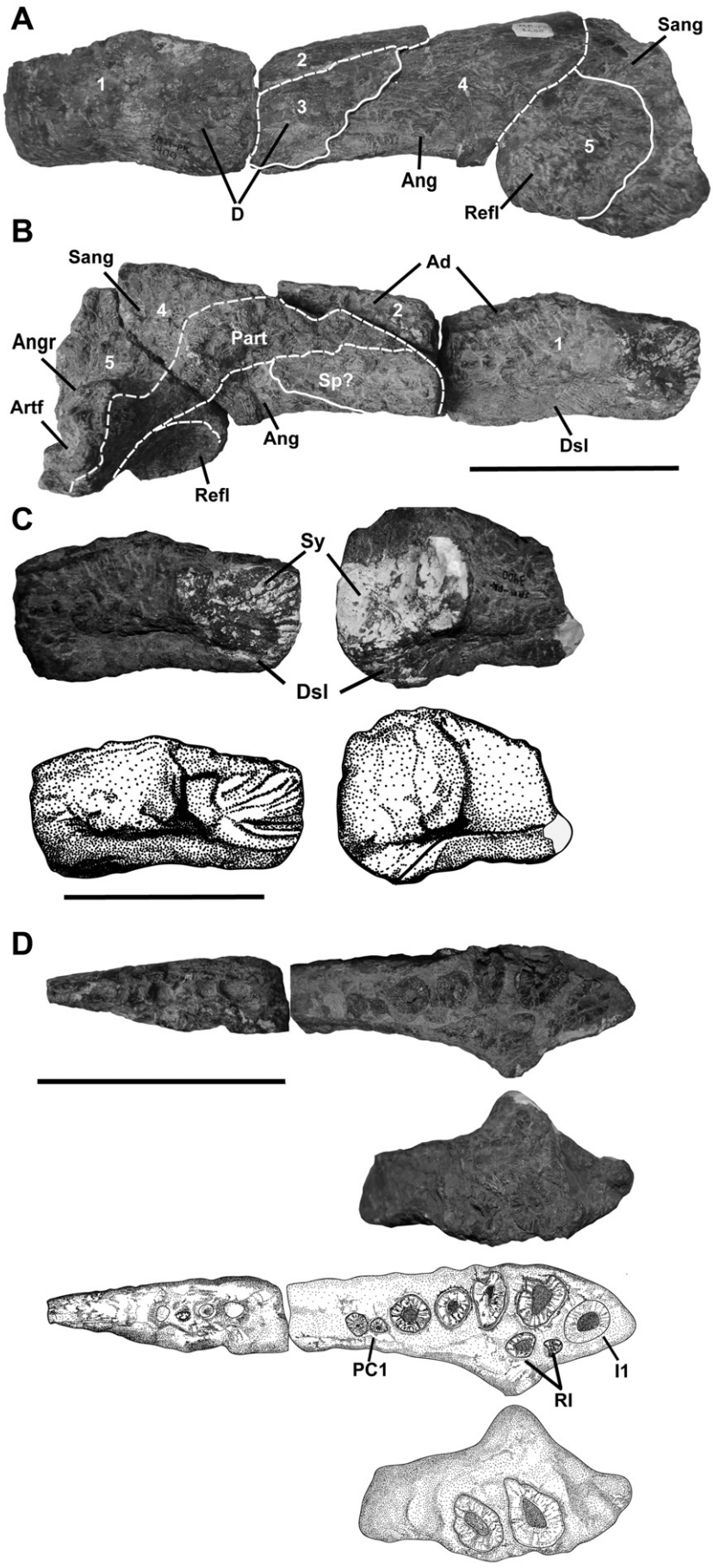

Figure 2. Photographs and drawings of the lower jaws of *Riebeeckosaurus longirostris* (SAM-PK-003400): lateral (**A**) and medial view (**B**) of left mandible; medial view (**C**) of symphysial portions of both sides of the mandible; note the deformation that resulted in both sides being strongly asymmetric; dorsal view (**D**) of the left mandible and anterior portion of the right mandible. Arabic numbers are fragments of the lower jaw. Dashed lines are interpreted sutures. Scale bars = 10 cm.

(Fig. 2C). The left anterior portion of the dentary bears the roots of four functional and, two replacement incisors, a canine, three postcanines and alveoli for three more postcanines, while the right portion bears two functional incisor root (Fig. 2D). Incisor roots are labiolingually elongated with the exception of the last incisor which is rounded in cross section and is similar in size to the canine root. Postcanine roots are significantly smaller than the canine root and the second postcanine root is relatively larger than the first one (Fig. 2D).

In lateral view, the dentary is a large bone comprising the entire anterolateral side of the lower jaw. Almost half way along the ventral length of the ramus the dentary meets the angular with an oblique suture, which slopes posterodorsally onto the surangular. The angular and the surangular are well exposed due to anterior displacement of the dentary. The posterodorsal portion of the dentary, which would have overlain the surangular (Fig. 2A) is not preserved, and as a result the angular makes up most of the posterolateral side of the jaw. There is a prominent and rounded reflected lamina. The angular is dorsally in contact with the surangular, the posterior margin of which is rather vertically oriented.

In medial view, the dentary also forms the anterior half of the lower jaw (Fig. 2B). The splenial is not preserved anteriorly, but the posterior end is a thin bone which tapers posteriorly and overlies the angular. A prominent articular, only visible from the medial side, is present on the posteroventral margin of the jaw and forms a well developed articular fossa bounded anteriorly by the prearticular. The prearticular sutures are not clearly represented and its anterior extension is inferred (Fig. 2B). This is a large and robust bone on the posterior half of the medial side of the jaw. This portion of the prearticular appears to be shorter and more vertically oriented than in lower jaws of other similar sized tapinocephalids. The prearticular swings anteriorly and appears to taper to a point half way along the jaw.

Avenantia kruisvleiensis

The holotype (SAM-PK-009166) consists of the posterior portion of the skull extending anteriorly as far as the level of the canine on the left side, and lacks a lower jaw (Figs 3–4). It has undergone significant distortion, which resulted in the skull being compressed dorsoventrally and the basicranium and the occiput being pushed upwards. Consequently, the occiput has been rendered almost continuous with the palate and the right temporal region has been displaced laterally. The intertemporal, interorbital and postorbital regions are represented by weathered cranial fragments, some of which were imperfectly glued together when the skull was reconstructed by Boonstra (1952b). Cranial roof thickening is weak to moderate when compared to that of other tapinocephalids, contra Boonstra (1952b, 1957), who considered it to be extensive. Post-burial deformation has caused lateral displacement of the left postfrontal and portions of the zygoma. This deformation resulted in exposure of the dorsomedial surface of the postorbital on the dorsal view, which would normally be situated medially in the temporal opening (see Boonstra 1952b, fig. 2, Boonstra 1957, fig. 11; Brink 1982). This opening is large and roomy, with anteroposterior diameter being larger than its dorsoventral diameter.

Skull roof and lateral view

The parietal is a relatively large bone forming the sagittal crest in the temporal region and broadening to its greatest width at the level of the pineal foramen. The parietal tapers anteriorly between the paired frontals (Fig. 3A), being thus different to the straight and transverse condition of the parietal-frontal suture described by Boonstra (1952b, 1957). The dorsal midline surface of the parietal is slightly concave in the area between the frontals and the prominent pineal foramen, which is situated on a slightly raised boss. As illustrated by Boonstra (1952b, 1957), the parietal makes up the dorsomedial surface of the temporal opening and is in contact anterolaterally with the postorbital, and posterolaterally with the squamosal. Posteriorly it wedges out between the tabular and the squamosal on the posterior branch of the temporal opening. The squamosal and parietal form a wide horizontal platform dorsally, which is exposed in the posterior portion of the temporal opening.

The frontal forms the greatest portion of the skull roof in the interorbital region. It is difficult to assess whether the frontal participates in the orbital margin, as the bones in the supraorbital region are fragmented and weathered but it appears that a limited contribution of the frontal on the right orbit is present (Fig. 3A). Likewise it is difficult to make a reliable assessment about the frontal contribution to the anterior margin of the temporal opening because this region of the cranium on both sides of the skull, is assembled by weathered and poorly fitting cranial fragments. Anteriorly it has a long anterior sutural contact with the prefrontal and also has a short medial contact with the posterior end of the nasal (Fig. 3A). The prefrontal is a relatively large and slightly thickened bone, which forms the largest part of the supraorbital margin. The left prefrontal is represented by an isolated bone fragment which has the same morphology as that of the right but has been weathered along sutural boundaries. The prefrontal slightly overhangs the posterior portion of the snout presenting a thickening that is continuous with the posterior end of the nasal (Boonstra 1952b, 1957).

The nasal, preserved only posteriorly and on the left, is displaced posteriorly together with a portion of the left prefrontal. Its posteriormost portion forms a narrow tongue between prefrontals and it meets the frontal at the level of the anterior margin of the orbit. The anterior contact of the nasal with the premaxilla is evidenced by a grooved impression on the right side of the nasal, corresponding to a posteromedial protrusion of the premaxilla which extends up to the end of the prefrontal (Fig. 3A).

The maxilla is preserved posteroventrally on both sides of the skull, and is more complete on the left side. On the ventral side of the left maxilla, three anterior teeth and succeeding alveoli for seven postcanines are preserved. The first tooth, adjacent to the maxillopremaxillary suture, is considerably larger than the next two and it is interpreted as a canine. Further preparation of the alveolus

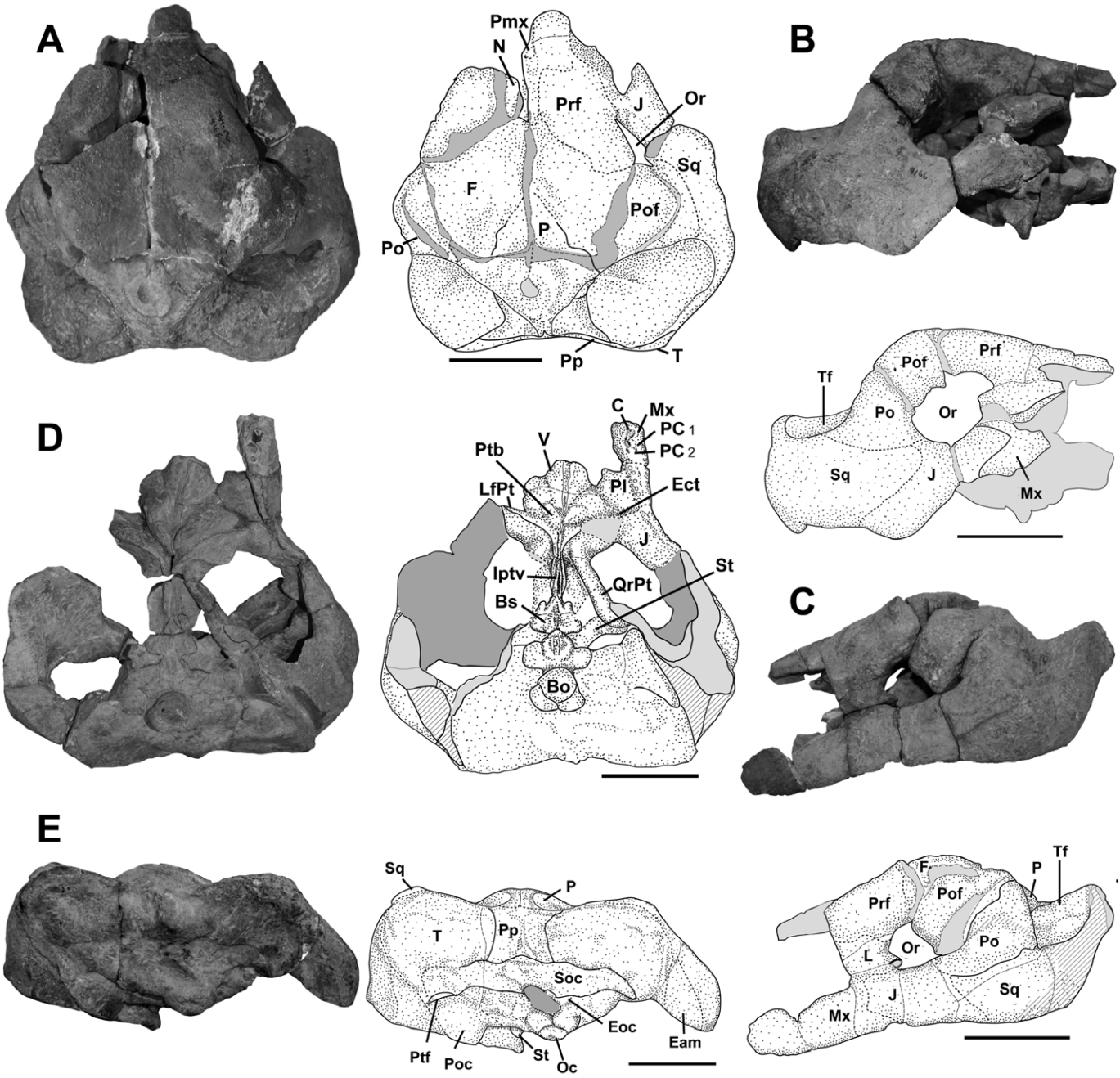

Figure 3. Photographs and drawings of dorsal (**A**), right (**B**), left (**C**), palatal (**D**) and occipital (**E**) view of SAM PK 009166 (holotype of *Avenantia kruisvleiensis*). Solid lines are visible and dashed lines are interpreted sutures. Narrow dashed lines are boundaries of bone fragments that correspond to cranial sutures except the one which extends across the parietal. Dark grey areas show internal view of cranium and breakage surfaces; light grey is plaster-reconstructed areas and matrix infilling; diagonal lines represent weathered bone surfaces. Scale bars = 10 cm.

revealed a partially erupted canine with a worn but distinctively denticulated mesiodistally but appears to lack a heel (Figs 3D & 4C). Only the first postcanine is well preserved, showing a triangular crown in lateral view and bearing denticles along the edge (Fig. 4A,B). The second postcanine is substantially smaller (Fig. 4A). The alveoli of the remaining postcanines are visible toward the posterior end of the maxilla (Fig. 3D).

Contrary to Boonstra's (1952b, 1957) description, the jugal forms the entire ventral margin of the orbit and presents an anterior spur-like contact with the maxilla, which continues anteriorly further than the anterior border of the orbit (Fig. 3B,C). The squamosal is a large bone forming the entire posterior and lateral margins of the temporal opening and having a long anterodorsal sutural contact with the postorbital.

Palate

Only the posterior portion of the palate is preserved, extending anteriorly up to the posterior end of the vomer. The vomer is paired, bearing a ventromedial trough that incorporates the midline suture with a weakly developed lateral ridge which does not extend as far as the posterior end of the vomer between the palatine bosses (Fig. 3D). The palatine is represented by a partial fragment and its sutural contacts are not clear. There is an anteroposteriorly elongated and bulbous palatine boss, lacking teeth. The posterior margin of the left choana is narrow and elon-

gated, formed equally by the vomer medially and the palatine laterally (Fig. 3D). A deeply positioned ectopterygoid is partially visible on the left side, anterior to the lateral process of the pterygoid. This is in contrast to Boonstra (1952b, 1957) and Brink (1982) who described this bone as being posterolateral to the process of the pterygoid, between the jugal and palatine.

The pterygoid is a tripartite bone comprising a central corpus, lateral process and the quadrate ramus. The central corpus has a midline suture and a narrow interpterygoidal vacuity that extends posteriorly along the midline from behind the lateral process up to the contact with the parasphenoidal rostrum. The pterygoid bosses are short and elongated in the same direction as the palatine bosses. A prominent lateral process, best preserved on the left, has a thin ventral ridge on its anterior margin which grades posteriorly into a horizontal shelf and posteromedially continues as a longitudinal ridge bordering the interpterygoidal vacuity. A posterolaterally directed, rather short, quadrate ramus meets the paraoccipital process of the opisthotic posterolaterally. It forms a strong ventral ridge, which merges anteriorly with the pterygoid corpus posterior to the lateral process (Fig. 3D).

Basicranium

The parasphenoid rostrum is preserved between the pterygoid bones on the posterodorsal portion of the basicranial girder and forms a pointed V-shaped midline contact with the pterygoid on the anterior side. The basisphenoid swells posterolaterally as far as the fenestra ovalis where it forms a transverse sutural contact with the basioccipital. A basisphenoid keel is present on the ventral midline, followed posteriorly by a basioccipital midline trough flanked by ridges, which diminishes as it extends posteriorly onto the basioccipital. Lateral to these structures, the basisphenoid and basioccipital form the tubera which attenuates posteriorly on both bones. The stapes (more completely preserved on the left side) are both located *in situ*. It is a short and stout rectangular bone with the proximal end located on the fenestra ovalis. Postmortem deformation of the stapes prevents further analysis of its morphology (Fig. 3D).

Occipital view

The entire occiput is preserved, but has been slightly dorsoventrally compressed, particularly on the right side, thus becoming laterally weakly concave (Fig. 3E). The occipital crest is slightly thickened on its posterior portion but it does not bend posteriorly towards the occiput, as described by Boonstra (1952b). The squamosal and part of the parietal form a rather horizontal platform which is exposed dorsally medial to the posttemporal arch. There is almost no convexity in the occiput and the occipital crest does not overhang the plate.

The postparietal is present as a relatively small, medially positioned and unpaired bone (Fig. 3E). Dorsally, it meets the posteroventral ends of the parietals and intrudes slightly between them, and contacts ventrally the supraoccipital. The postparietal has a crested midline ridge, which extends dorsoventrally across the entire bone surface, but becomes less prominent onto the dorsomedial side of the supraoccipital. A large and flat tabular bone forms the dorsolateral portion of the occipital plate. Dorsally it has a long sutural contact with the parietal,

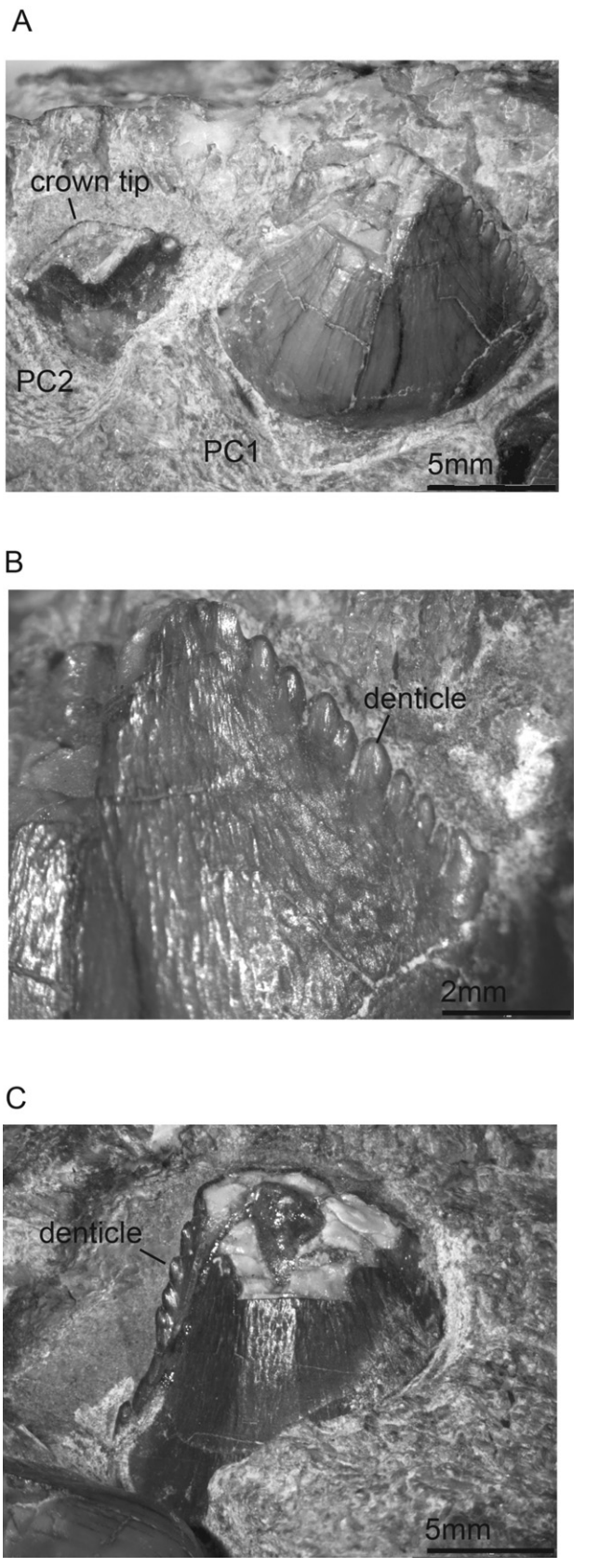

Figure 4. Photographs of dentition of SAM-PK-009166: lateral view of postcanines 1 and 2 (**A**); detail of denticles on the crown of the first postcanine in lateral view (**B**) and lingual view of the canine (**C**).

which is visible in dorsal view (Fig. 3A). Ventrolaterally a long spur of the tabular extends between the external auditory meatus and the supraoccipital as a long ribbon-shaped element, which is in contact with the postparietal dorsomedially. The ventral portion of the supraoccipital forms the dorsal margins of the posttemporal fenestra and the foramen magnum. Towards the ventrolateral end of the supraoccipital, Boonstra (1952b, 1957) illustrated a long horizontal sutural contact between the supraoccipital and the paraoccipital process of the opisthotic. However, we interpret this contact as being very short (Fig. 3E).

The exoccipital has a short wing-like morphology lateral to the foramen magnum of which it forms the lateral and ventral borders (Fig. 3E). This bone is in line with the supraoccipital, having a rather short contact between them. A clear tripartite occipital condyle is present, with a contribution from the basioccipital. Due to distortion, the paraoccipital process appears to almost contact the medial surface of the dorsal process of the quadrate, whereas the distal margin of the left paraoccipital process, broken in two pieces, ends near the distal margin of the stapes (Fig. 3D,E). The left paraoccipital process overhangs distally the occipital portion of the squamosal and forms part of the medial margin of the external auditory meatus. The left quadrate is partially preserved, its dorsal process being in contact dorsolaterally with the squamosal and medially with the quadrate process of the pterygoid. The quadratojugal is not preserved.

DISCUSSION

Re-examination of the holotypes of *Avenantia kruisvleiensis* and *Riebeeckosaurus longirostris* shows that some of the features which were considered diagnostic for these taxa are in fact not unique to them, whereas others are indeed a by-product of the poor preservation of the specimens. Thus, the heavily weathered nature of the skull roof of the holotype of *A. kruisvleiensis* significantly influenced previous interpretation of its morphology. For example, the described features such as the distinct 'ring wall' surrounding the pineal opening, and the 'low intertemporal crest' included in the diagnosis by Boonstra (1952b, pp. 250, 254, 255, and 1957, pp. 19, 35) appear to be the remnant of a raised pineal opening rim and a once prominent intertemporal crest (like the one which is observed in *Riebeeckosaurus*) which was weathered away. Other alleged diagnostic characters of *A. kruisvleiensis*, such as the contribution of the exoccipital to the occipital condyle and the contact between the squamosal and postorbital along the temporal opening, are also features which are observed in other tapinocephalids such as *Tapinocaninus* (S.G., pers. obs.) and *Moschops* (e.g. Boonstra 1957).

Of great taxonomic consequence is the inferred condition of a long snout for *Riebeeckosaurus longirostris*, which besides being considered diagnostic for this species, led to its being considered in a separate taxonomic group to *Avenantia kruisvleiensis* (Boonstra 1952a, 1963b, 1969; King 1988). There is no preservation of the snout in any specimen of *R. longirostris,* and the assumption of a long snout was based on the length of the lower jaw of the holotype of *R. longirostris*. Barghusen (1975, p. 298) however, considered that the dentary has been 'displaced forward relative to the postdentary bones as a result of a distortion,' thus increasing the apparent length of the lower jaw. The comparison of the lower jaw of *R. longirostris* with that of a similar sized specimen of the well-known short-snouted *Moschops* reveals that there is little difference in length between these elements.

From our detailed analysis of the specimens attributed to *A. kruisvleiensis* and *R. longirostris,* it is evident that these taxa are very similar in morphology and share the following characters: a relatively large and mediolaterally and anteroposteriorly expanded temporal opening which is similar to *Tapinocaninus*; the presence of an intertemporal crest; a weak concavity of the occiput in posterior view; anterior position of the quadrate condyles extended anteriorly below the orbit (the position of this bone is inferred for *A. kruisvleiensis* after the orientation of the squamosal); weak thickening on the dorsal portion of the occipital crest; wide exposure of the parietal lateral to the sagittal crest on the medial portion of the temporal fossa. Some of the above-mentioned features in *R. longirostris* and *A. kruisvleiensis*, such as the narrow intertemporal region and relatively large temporal openings are similar to the condition observed in the basal tapinocephalid *Tapinocaninus* but the former taxa show a more developed sagittal crest and a less prominent but wider ridge of the squamosal on the dorsomedial portion of the temporal opening.

Despite some similarity to the basal tapinocephalid *Tapinocaninus,* the latter is known from the *Eodicynodon* Assemblage Zone (AZ). In contrast the specimens of *R. longirostris* and *A. kruisvleiensis* come from localities which are stratigraphically high in the Abrahamskraal Formation, corresponding to the top of the *Tapinocephalus* AZ (M. Day, pers. comm. 2010).

The characters differentiating *A. kruisvleiensis* from *R. longirostris* can be explained by distortion or weathering. Main differences of *A. kruisvleiensis* in comparison with *R. longirostris* are: an anteroposteriorly longer temporal opening; absence of thickening of the parietal surface in front of the pineal opening; a reduced postorbital bar and a rounded lower corner of the posterior margin of the zygoma in lateral view. Some of these character variations have also been observed between similar sized, subadult to adult specimens of *Moschops* and *Tapinocaninus* which suggest that such differences could be linked with sexual dimorphism (in particular, differences in the pachyostotic development of the postorbital bar), or individual variation.

The morphological similarity between the skulls of *Riebeeckosaurus longirostris* and *Avenantia kruisvleiensis* lead us to conclude that they belong to the same species. This is strengthened by the close geographic and stratigraphic proximity of their localities which are both situated at the top of the *Tapinocephalus* AZ. As the name *Riebeeckosaurus longirostris* has priority under Article 23 of the Code of Zoological Nomenclature, this is the name that will be retained, with *Avenantia kruisvleiensis* becoming the junior synonym.

SYSTEMATIC PALAEONTOLOGY

Therapsida Broom, 1905
Dinocephalia Seeley, 1894
Tapinocephalia Broom, 1923
Tapinocephalidae Lydekker, 1890

Riebeeckosaurus Boonstra, 1952a
Syn. *Avenantia* Boonstra, 1952b

Revised diagnosis of Riebeeckosaurus

Short-snouted tapinocephalid that can be distinguished from others members of the family by the presence of crest like intertemporal region; parietals bends moderately backward on the intertemporal area posterior to the pineal opening; and lacking the squamosal facet between the squamosal and pararoccipital end laterally. It can be distinguished from all except *Tapinocaninus* by having canine differentiation; wide temporal fossa; wide platform formed on the dorsomedial portion of the temporal opening, where the parietal and squamosal meet on the medial side of the posttemporal arch.

Type species

Riebeeckosaurus longirostris Boonstra, 1952a
Syn. *Avenantia kruisvleiensis* Boonstra, 1952b

Holotype

SAM-PK-003400, posterior half of the cranium and a lower jaw fragments (Figs 1–3).

Type locality

Boonstra (1952a) gives the locality as close to Viviershalte, Beaufort West. The farm name is recorded as Leeuwkraal (with Viviers as an alternative name in the Karoo vertebrate database at the Evolutionary Studies Institute of the Witwatersrand University.)

Referred specimens

SAM-PK-011955, posterior portion of a skull roof (Fig. 1A). Boonstra (1952a) gives the location as the Koup, which is a flat area between Beaufort West and a southward projection of high ground about 30 km east of Laingsburg, bounded on the north by the Great escarpment and the south by the Swartberg mountains. SAM-PK-009166 (holotype of *A. kruisvleiensis*), skull (lacking snout and lower jaw, Figs 3–4) and some postcranial fragments including a femoral head. From the farm Kruisvlei, near Merweville, Beaufort West (Boonstra 1952b). SAM-PK-009167, postcranial bones (scapula, ilium and femur). From the farm Kruisvlei near Merweville Beaufort West (Boonstra 1955). There is no cranial material associated to this specimen, thus the taxonomic identification of this material is only tentative, and final confirmation will require additional discoveries of *R. longirostris*.

It is interesting that Boonstra (1955) quoted SAM-PK-009167 as the holotype of *A. kruisvleiensis* instead of SAM-PK-009166, which was considered a mistake by van den Heever and Grine (1981). In the same contribution, Boonstra (1955) mentions an associated cranium under SAM-PK-9167.

Stratigraphic information

All specimens occur stratigraphically high in the *Tapinocephalus* AZ, towards the top of the Abrahamskraal Formation of the Beaufort Group (M. Day, 2011, pers. comm.) and have been found in close proximity to specimens of *Moschops*. The locality of SAM-PK-011955 is listed only as the Koup which is an extensive area covering various stratigraphic levels of the *Tapinocephalus* AZ.

Comment

Riebeeckosaurus longirostris and *A. kruisvleiensis* were described in the same volume (12, no. 2) of the *Tydskrif vir Wentenskap en Kuns* (Journal for Science and Art – South African Academy for Science and Art). *Avenantia* was mentioned in the description of *R. longirostris,* but the fact that the mention of the name lacked a prior description and reference (Article 13 of the Code of Zoological Nomenclature) that makes the name a *nomen nudum* (see also van den Heever & Grine 1981). As the description of *A. kruisvleiensis* was published after the description of *R. longirostris,* the latter species has priority under the Code of Zoological Nomenclature – Article 23.

CONCLUSIONS

From the detailed morphological comparison it is clear that the holotype and only representative of *Avenantia kruisvleiensis* (SAM-PK-009166) shares several cranial and dental features with the holotype and referred specimens of *Riebeeckosaurus longirostris* (SAM-PK-003400 and SAM-PK-011955). Accordingly we consider *A. kruisvleiensis* to be a junior synonym of *R. longirostris* and contrary to the most previous proposals the species should be included in the short-snouted tapinocephalid taxa. The morphological differences that are observed between the two genera (e.g. surface thickening of parietal, postorbital bar and general cranial thickening) are best interpreted as being the result of sexual or ontogenetic variation. The fact that the specimens are of similar size suggests that the former is more likely.

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ABBREVIATIONS

Institutional

SAM Iziko, South African Museum, Cape Town, South Africa;
NMQR National Museum Bloemfontein, Bloemfontein, South Africa.

Anatomical

Ad	alveolar margin of dentary	Dsl	dentary sulcus
AMx	alveolar margin of maxilla	Ect	ectopterygoid
Ang	angular	Eo	exoccipital
Angr	angular ridge	Eam	external auditory meatus
Artf	articular fossa	F	frontal
Bo	basioccipital	I_1	first incisor
Bs	basisphenoid	Iptv	interpterygoid vacuity
C	canine	J	jugal
D	dentary	L	lacrimal

Lfpt lateral flange of pterygoid
Mx maxilla
N nasal
Or orbit
Oc occipital condyle
P, parietal
Part prearticular
Pl palatine
Pc1 and Pc2, postcanine 1 and 2
Pmx premaxilla
Po postorbital
Poc paraoccipital process
Pof postfrontal
Pp postparietal
Prf prefrontal
Ptb palatine boss
Ptf posttemporal foramen
Q quadrate
Qrpt quadrate ramus of pterygoid
Refl reflected lamina
RI replacement incisors
Sang surangular
So supraoccipital
Sp splenial
Sq squamosal
St stapes
Sy symphysis of the lower jaw
T tabular
Tf temporal fossa
V vomer

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